

# Terrestrial biosphere models underestimate photosynthetic capacity and CO<sub>2</sub> assimilation in the Arctic

Alistair Rogers<sup>1</sup>, Shawn P. Serbin<sup>1</sup>, Kim S. Ely<sup>1</sup>, Victoria L. Sloan<sup>2</sup> and Stan D. Wullschleger<sup>2</sup>

<sup>1</sup>Environmental and Climate Sciences Department, Brookhaven National Laboratory, Upton, NY 11973-5000, USA; <sup>2</sup>Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831-6301, USA

Author for correspondence:

Alistair Rogers

Tel: +1 631 344 2948

Email: arogers@bnl.gov

Received: 6 June 2017

Accepted: 8 July 2017

*New Phytologist* (2017) **216**: 1090–1103

doi: 10.1111/nph.14740

**Key words:** earth system models, maximum carboxylation capacity ( $V_{c,max}$ ), maximum electron transport rate ( $J_{max}$ ), photosynthesis, Rubisco, temperature response function, tundra.

## Summary

- Terrestrial biosphere models (TBMs) are highly sensitive to model representation of photosynthesis, in particular the parameters maximum carboxylation rate and maximum electron transport rate at 25°C ( $V_{c,max,25}$  and  $J_{max,25}$ , respectively). Many TBMs do not include representation of Arctic plants, and those that do rely on understanding and parameterization from temperate species.
- We measured photosynthetic CO<sub>2</sub> response curves and leaf nitrogen (N) content in species representing the dominant vascular plant functional types found on the coastal tundra near Barrow, Alaska.
- The activation energies associated with the temperature response functions of  $V_{c,max}$  and  $J_{max}$  were 17% lower than commonly used values. When scaled to 25°C,  $V_{c,max,25}$  and  $J_{max,25}$  were two- to five-fold higher than the values used to parameterize current TBMs. This high photosynthetic capacity was attributable to a high leaf N content and the high fraction of N invested in Rubisco. Leaf-level modeling demonstrated that current parameterization of TBMs resulted in a two-fold underestimation of the capacity for leaf-level CO<sub>2</sub> assimilation in Arctic vegetation.
- This study highlights the poor representation of Arctic photosynthesis in TBMs, and provides the critical data necessary to improve our ability to project the response of the Arctic to global environmental change.

## Introduction

Carbon (C) uptake and loss from high-latitude ecosystems are highly sensitive to climate change, and these processes are poorly represented in Earth system models. The Arctic has experienced the greatest regional warming (Kaufman *et al.*, 2009) and is projected to warm twice as much as the rest of the planet by the end of the century (IPCC, 2013). The resulting widely observed permafrost thaw and degradation are projected to continue as the region warms, leading to the release of large amounts of stored C into the atmosphere (Jorgenson *et al.*, 2006; Schuur *et al.*, 2009, 2015; Koven *et al.*, 2015). At the same time, rising carbon dioxide concentration ([CO<sub>2</sub>]), increasing temperature and increased nitrogen (N) availability may stimulate CO<sub>2</sub> uptake and lead to a continued and enhanced ‘greening’ of the Arctic landscape, creating critical uncertainty over the future of the Arctic C cycle (Sturm *et al.*, 2001; Tape *et al.*, 2006; Frost & Epstein, 2014; Salmon *et al.*, 2016). Accurate projection of C fluxes at high latitudes will require improved model representation of these processes in terrestrial biosphere models (TBMs). A recent analysis has demonstrated that, in current TBMs, photosynthesis remains a dominant source of C cycle uncertainty in the Arctic (Fisher *et al.*, 2014).

Leaf-level photosynthesis is represented in many TBMs by the Farquhar, von Caemmerer and Berry (FvCB) model (Farquhar *et al.*, 1980; von Caemmerer, 2000). Two key parameters required by the FvCB model are the maximum carboxylation rate ( $V_{c,max}$ ) by the photosynthetic enzyme Rubisco (EC number 4.1.1.39) and the maximum electron transport rate ( $J_{max}$ ) associated with regeneration of the CO<sub>2</sub> acceptor molecule ribulose-1,5-bisphosphate (RuBP). Currently, most TBMs use plant functional types (PFTs) to represent the vegetation present in different biomes, and these PFTs are parameterized with traits that are used to model the CO<sub>2</sub> uptake of the vegetation in a given biome. There are a range of alternative approaches that seek to replace PFTs with a ‘trait-based’ approach in future TBMs (Wullschleger *et al.*, 2014). However, these approaches, such as trait–environment linkages (e.g. van Bodegom *et al.*, 2014), trait filtering (e.g. Fisher *et al.*, 2012) and optimality approaches (e.g. Xu *et al.*, 2012), still use an FvCB approach to represent photosynthesis, and still need data to inform parameterization, model development and to evaluate prognostic traits. In current TBMs,  $V_{c,max}$  at 25°C ( $V_{c,max,25}$ ) is typically a PFT-specific model input, whereas  $J_{max}$  at 25°C ( $J_{max,25}$ ) is commonly calculated from the PFT-specific  $V_{c,max,25}$  using a TBM-specific ratio between  $J_{max,25}$  and  $V_{c,max,25}$  ( $JV_{ratio,25}$ ). The  $JV_{ratio}$  has also been used in the

opposite direction to estimate  $V_{c,max}$  from remotely sensed chlorophyll content (Alton, 2017). Based on previous analysis (Wullschlegel, 1993),  $JV_{ratio,25}$  has long been assumed to be constant for all PFTs, but has been shown to decrease with increasing growth temperature (Kattge & Knorr, 2007). Critically,  $JV_{ratio,25}$  can have a significant impact on photosynthetic  $CO_2$  responsiveness, with a higher  $JV_{ratio,25}$  enabling a more responsive Rubisco-limited increase in photosynthesis as  $[CO_2]$  rises (Rogers *et al.*, 2017c). In TBMs, photosynthesis is particularly sensitive to the temperature response functions (TRFs) used to scale both  $V_{c,max}$  and  $J_{max}$  from the reference temperature, usually 25°C, to growth temperature. However, these TRFs are typically assumed to be identical for all PFTs (Rogers *et al.*, 2017c). Mounting evidence has shown that this is not a valid assumption and there is an ongoing effort in the community to capture PFT-specific TRFs for use in TBMs (Medlyn *et al.*, 2002; Varhammar *et al.*, 2015; Galmes *et al.*, 2016). This is particularly important for the Arctic, because widely used TRFs have been derived from measurements made on temperate species and do not include measurements made below 10°C, a typical growth temperature for Arctic species (Bernacchi *et al.*, 2001, 2003).

Sensitivity analysis, model simulations and efforts to identify model parameter uncertainty have repeatedly shown that model projections of gross and net primary productivity are particularly sensitive to  $V_{c,max,25}$ , and the parameters used to estimate it (Friend, 2010; Bonan *et al.*, 2011; Lebauer *et al.*, 2013; Sargsyan *et al.*, 2014). Moreover, previous studies have also shown that model uncertainty in plant productivity can be significantly reduced through the incorporation of PFT-specific measured values of  $V_{c,max}$  (Dietze *et al.*, 2014). However, a recent examination of the derivation of  $V_{c,max}$  in 10 TBMs revealed that most models do not have an explicit Arctic PFT and the four models that do include an Arctic PFT rely on limited or inappropriate datasets to estimate Arctic  $V_{c,max,25}$  (Rogers, 2014).

There is a rich history of ecological research in the Arctic, including many studies that have measured photosynthesis (Wookey *et al.*, 1995; Chapin & Shaver, 1996; Muraoka *et al.*, 2002, 2008; Starr & Oberbauer, 2003; Starr *et al.*, 2004; Reich *et al.*, 2009; Albert *et al.*, 2011; Boesgaard *et al.*, 2012; Fletcher *et al.*, 2012; Leffler & Welker, 2013; Patankar *et al.*, 2013; Heskell *et al.*, 2014; Souther *et al.*, 2014; Saarinen *et al.*, 2016). However, at the time we began this study, there were no published data on  $V_{c,max}$  or  $J_{max}$  measured in Arctic vegetation that could be used to inform the representation of Arctic photosynthesis in TBMs and, to the best of our knowledge, only one other study emerged after we began our work (van de Weg *et al.* 2013). In short, the data needed to understand and parameterize a key process that has been demonstrated to be driving marked uncertainty in TBM projections of the C cycle in a critical biome are essentially missing.

We hypothesized that current TBM representation and parameterization of photosynthesis, which is based largely on knowledge gained in temperate systems, will be markedly different for Arctic vegetation. The goal of this study was to increase our understanding of photosynthesis in the Arctic and to provide new data and insights that could be used to reduce uncertainty in

TBM projections of photosynthesis in the Arctic, either directly through improved parameterization of the Arctic PFT, or indirectly through the evaluation of emergent model states that result from alternative ‘trait-based’ modeling approaches (prognostic photosynthetic parameters). In this study, we provide the first Arctic dataset on the critical photosynthetic traits  $V_{c,max,25}$  and  $J_{max,25}$ , their TRFs and associated biochemical and structural traits; and compare these data with the parameterization currently used in TBMs, including the use of plant traits to derive photosynthetic parameters.

## Materials and Methods

### Plant material

This study was conducted on the coastal tundra at the Barrow Environmental Observatory (BEO), near Barrow, AK (71.3°N, 156.5°W; note that, on 1 December 2016, Barrow was officially renamed Utqiagvik following the original Inupiat name), USA. The BEO landscape is characterized by small thaw ponds and low- and high-centered polygons with a low vascular plant species diversity that is dominated by *Carex aquatilis* (Brown *et al.*, 1980). Mean annual air temperature is −12°C (annual range, 31°C) and mean annual precipitation is 106 mm, with the majority falling as rain during the short summer. Soils are generally classified as Gelisols, underlain by permafrost which extends to depths of 300 m or greater, with an active layer thickness of 20–70 cm (Brown *et al.*, 1980; Bockheim *et al.*, 1999; Shiklomanov *et al.*, 2010).

The measurement of leaf traits and gas exchange was conducted over an area of c. 1 km<sup>2</sup> centered at 71.28°N, 156.65°W. This area was characterized by zones of disturbance and significant permafrost degradation, standing water, dry, high-centered polygons as well as relatively undisturbed low-centered polygonal ground that collectively provided diverse microtopography and drainage, and therefore highly suitable habitats for large stands of the different species of interest. Our goal was to measure key traits in the dominant vascular plants in this landscape, but also in those plants that represented key Arctic PFTs (Chapin *et al.*, 1996). Our choice of species was also constrained by practical limitations of the gas exchange instrumentation: for example, the ability to clamp on a leaf with sufficient leaf area to provide an acceptable signal-to-noise ratio that enabled us to measure a  $CO_2$  response curve. We studied seven species covering four Arctic PFTs: grasses, *Arctagrostis latifolia* (R.Br.) Griseb., *Arctophila fulva* (Trin.) Andersson, *Dupontia fisheri* R.Br.; sedges, *Carex aquatilis* Wahlenb., *Eriophorum angustifolium* Honck.; forbs, *Petasites frigidus* (L.) Fr.; and deciduous shrubs, *Salix pulchra* Cham. As a result of the clonal nature of these species, it was not possible to determine whether individual ramets were genetically distinct. Therefore, stands separated by geomorphological features, i.e. different polygonal units or thaw ponds, were chosen to increase the likelihood that they were not members of the same clonal colony (Shaver *et al.*, 1979). Measurements were taken between 10 July and 10 August (2012–2016), a period characterized by cool temperatures and continuous daylight. The bulk of

our measurements were focused on the period of the peak biomass (mid to late July), when the first mature leaves in these species are available for gas exchange, but before the onset of leaf senescence. As a result of the scarcity of individuals of some species (*S. pulchra*), additional data collection associated an effort to link leaf spectral signatures with physiology (Serbin *et al.*, 2012) and the challenge of taking good measurements (*D. fisheri*), our replication within a species varied (*A. latifolia*,  $n=13$ ; *A. fulva*,  $n=26$ ; *C. aquatilis*,  $n=36$ ; *D. fisheri*,  $n=8$ ; *E. angustifolium*,  $n=43$ ; *P. frigidus*,  $n=44$ ; *S. pulchra*,  $n=9$ ).

### Gas exchange and derived parameters

Gas exchange measurements were made in the field using two to five LI-6400XT gas exchange systems (Li-Cor, Lincoln, NE, USA) that were zeroed at the field site with a common nitrogen standard (99.9998%  $N_2$ ,  $CO_2 < 0.5$  ppm,  $H_2O < 0.5$  ppm; Alphagaz 2, Air Liquide American Specialty Gases LLC, Anchorage, AK, USA). We measured the response of photosynthesis ( $A$ ) to intercellular  $CO_2$  concentration ( $C_i$ ), commonly called  $A-C_i$  curves. Leaf chamber temperature was maintained at ambient temperature using the Peltier-based temperature control of the gas exchange system by setting the chamber block temperature to match the air temperature measured using the leaf thermocouple with the chamber open. The water vapor pressure of air entering the chamber was not controlled and therefore matched ambient conditions. However, on cold, high-humidity days, the block temperature was set to 0.5–1.5°C above ambient air temperature to increase the differential between the dew point temperature and the chamber block temperature in order to eliminate the chance of condensation inside the instrument. Even with this slight increase in temperature, the leaf water vapor pressure deficit ( $VPD_{leaf}$ ) was always below 1.0 kPa and, typically,  $c. 0.3$  kPa. All measurements were made on fully expanded leaves. When the leaf did not completely fill the leaf chamber of the instrument, which was the case for all the graminoid species, the leaf material protruding from the chamber was marked at the edge of the gasket to identify the section that was enclosed in the chamber. The leaf was then removed from the chamber and plant, and the enclosed section was measured indoors with a ruler and hand lens to allow the determination of the leaf width to the nearest 0.25 mm. The leaf width was then used to calculate the leaf area enclosed by the leaf chamber, and gas exchange data were recomputed using the measured leaf area.

During the period of measurement, the Arctic experiences 24 h of daylight. As a result, transient decreases in chloroplast inorganic phosphate concentration and photosystem II efficiency, which can occur shortly after initial illumination, and which may alter the response of  $A$  to  $C_i$ , are not a concern (Ainsworth *et al.*, 2003). In addition, attempts to remove plant material from the field and to conduct measurements indoors, where marked temperature manipulation would be possible, were unsuccessful. Therefore,  $A-C_i$  curves were all measured *in situ*. Preliminary light response curves, in which we carefully controlled for  $CO_2$  concentration and leaf temperature, indicated that, despite expectations, these Arctic species did not

photosaturate below  $1500 \mu mol m^{-2} s^{-1}$ . Therefore, we used an irradiance of  $2000 \mu mol m^{-2} s^{-1}$  for our light-saturated measurements. The differential between sample and reference infrared gas analyzers (IRGAs) was maximized using the  $2 \times 3$ -cm<sup>2</sup> leaf chamber to increase potential leaf area, and by lowering the flow rate (typically to  $350 \mu mol s^{-1}$ ) until the  $CO_2$  differential between sample and reference chambers was  $c. 10 \mu mol CO_2 mol^{-1}$  at a  $CO_2$  reference chamber set point of  $400 \mu mol mol^{-1}$  and saturating irradiance. This ensured a good signal-to-noise ratio at low  $[CO_2]$ . After clamping on a leaf, the chamber was leak tested by vigorously blowing through a tube directed at the margins of the gasket. When leaks were identified (fluctuations in  $[CO_2]$  in the sample cell  $> 1 \mu mol mol^{-1}$  over 15 s), the leaf was repositioned or leaks were sealed with a silicone compound (Molykote 111; Dow Corning, MI, USA). Following the established procedure (Long & Bernacchi, 2003; Bernacchi *et al.*, 2006), each leaf was first allowed to achieve steady-state  $CO_2$  and water vapor exchange. The minimum amount of time allowed for stabilization was 20 min, but, typically, we waited more than 30 min. The reference  $[CO_2]$  was then reduced stepwise to  $50 \mu mol mol^{-1}$ , returned to  $400 \mu mol mol^{-1}$  and then increased stepwise to  $1800 \mu mol mol^{-1}$ . Each individual curve consisted of 13 separate  $CO_2$  set points and included multiple set points at a  $[CO_2]$  value of  $400 \mu mol mol^{-1}$  to allow for potential recovery from low  $[CO_2]$ . Response curves were measured rapidly to avoid acclimation to a given set point. Following an adjustment to a new  $[CO_2]$  value, data were logged as soon as the  $[CO_2]$  in the reference cell was stable ( $SD < 0.75 \mu mol mol^{-1}$  over 20 s). Following equilibration, each curve took  $c. 30$  min to complete.

In addition to making measurements at ambient growth temperature in all species, we also measured  $A-C_i$  response curves at multiple temperatures on the same leaf in *P. frigidus* and *E. angustifolium* in order to expand the temperature range of our dataset. This was achieved using the cooling and heating feature of the gas exchange system. In some cases, we focused on the initial slope of this response to speed up measurements and, as a result, collected more data on the temperature response of  $V_{c,max}$  than  $J_{max}$ . In each case, following the completion of a full or partial  $CO_2$  response curve, the leaf temperature was increased by  $c. 5^\circ C$  and allowed to stabilize for a minimum of 20 min before a new response curve was measured. At our high-temperature limit ( $25^\circ C$ ),  $VPD_{leaf}$  did not rise above 1.75 kPa. Analysis of the data from a nearby flux tower (Torn *et al.*, 2014 and unpublished data) showed that mean daily air temperatures on the days preceding our measurements were similar ( $3.7 \pm 2.5$  SD (5-d average),  $4.3 \pm 2.0$  SD (10-d average),  $4.3 \pm 1.7$  SD (30-d average)), giving us confidence that, when combining our full dataset for the analysis of temperature response functions, there would be no marked impact of potential thermal acclimation to the air temperature of the days preceding our measurements.

The photosynthetic parameters  $V_{c,max}$  and  $J_{max}$  were estimated based on the equations originally described by Farquhar *et al.* (1980), where  $A$  is the minimum of the RuBP-saturated  $CO_2$

assimilation rate ( $A_c$ ) and the RuBP-limited  $\text{CO}_2$  assimilation rate ( $A_j$ , Eqn 1).

$$A = \min(A_c, A_j) \quad \text{Eqn 1}$$

Triose phosphate utilization (TPU) limitation can also be a third limitation on  $A$ , but usually occurs at a higher than physiologically relevant  $\text{CO}_2$  concentration (Sharkey, 1985). We saw no evidence of TPU limitation of  $A$  in our  $A-C_i$  curves, despite the low measurement temperatures. One possible explanation for the absence of TPU limitation is the large root : shoot ratio (Iversen *et al.*, 2015), and hence sink capacity, in Arctic species which would limit the potential feedback inhibition of photosynthesis by minimizing the buildup of triose phosphate in the leaves. Therefore, we did not include TPU limitation in our model formulation for the estimation of  $V_{c,\max}$  and  $J_{\max}$ . We did not account for the influence of mesophyll conductance on the estimates of  $V_{c,\max}$  and  $J_{\max}$ , and thus our reported 'apparent' values are based on intercellular as opposed to chloroplastic  $[\text{CO}_2]$ .

Apparent  $V_{c,\max}$  and apparent  $J_{\max}$  were determined based on  $C_i$ , as described previously, using the commonly employed method of separate fitting of  $A$  to  $C_i$  for Rubisco and RuBP regeneration-limited  $A$  (Farquhar *et al.*, 1980; Bernacchi *et al.*, 2013).  $A_c$  was modeled based on Eqn 2, where  $C_i$  and  $O_i$  are the intercellular  $\text{CO}_2$  and  $\text{O}_2$  concentrations ( $O_i = 210 \text{ mmol mol}^{-1}$ ), respectively,  $\Gamma^*$  is the  $\text{CO}_2$  compensation point in the absence of non-photorespiratory mitochondrial respiration in the light, and  $K_c$  and  $K_o$  are the Michaelis–Menten coefficients of Rubisco activity for  $\text{CO}_2$  and  $\text{O}_2$ , respectively. We used the NADPH-limited version of the equation used to describe the electron transport rate in the determination of the RuBP-limited  $\text{CO}_2$  assimilation rate ( $A_j$ , Eqn 3), and employed the values and temperature sensitivities of  $K_c$ ,  $K_o$  and  $\Gamma^*$  from Bernacchi *et al.* (2001).

$$A_c = \frac{(C_i - \Gamma^*) V_{c,\max}}{K_c \left(1 + \frac{O_i}{K_o}\right) + C_i} - R_d \quad \text{Eqn 2}$$

$$A_j = \frac{(C_i - \Gamma^*) J}{4C + 8\Gamma^*} - R_d \quad \text{Eqn 3}$$

We parameterized Eqns 2 and 3 of the FvCB model, using a custom program (<https://github.com/TESTgroup-BNL/R-GasExchange/releases/tag/0.8>) developed within the R statistical environment (R Development Core Team, 2013), to calculate the optimum apparent  $V_{c,\max}$ , apparent  $J_{\max}$  and leaf respiration for each  $A-C_i$  curve. Our model fitting utilized the derivative evolution (DE) algorithm (Price *et al.*, 2006), implemented in the R package 'DEOPTIM' (Ardia, 2009), to minimize the difference between the modeled and observed photosynthetic rate to derive the optimum apparent  $V_{c,\max}$  and apparent  $J_{\max}$  for each  $A-C_i$  curve. The DE algorithm is a stochastic, population-based optimizer, which seeks the global minimum of the objective

function without the need for arbitrary initial parameter values which can result in errors in optimization (Dubois *et al.*, 2007). Our parameter optimization strategy was implemented to avoid the co-limited region of the  $A-C_i$  response curve, which, for these Arctic species, was at a high  $C_i$ :  $V_{c,\max}$  was estimated from the lower portion of the  $A-C_i$  curve ( $C_i < 400 \text{ Pa}$ ) and  $J_{\max}$  was estimated from the upper portion of the curve ( $C_i > 650 \text{ Pa}$ ).

The temperature responses of  $V_{c,\max}$  and  $J_{\max}$  were determined by fitting measured values against the mean  $T_{\text{leaf}}$  for each individual  $A-C_i$  response curve, as described previously (Medlyn *et al.*, 2002), which allowed us to estimate the activation energy ( $E_a$ ) associated with  $V_{c,\max}$  and  $J_{\max}$ . We then used Eqn 4 (shown for  $V_{c,\max}$ ) to scale the measured  $V_{c,\max}$  at  $T_{\text{leaf}}$  ( $V_{c,\max,T}$ ) to  $V_{c,\max}$  at  $25^\circ\text{C}$  ( $V_{c,\max,25}$ ).  $T_{\text{leaf}}$  was expressed in K and  $R$  is the universal gas constant ( $8.314 \text{ J mol}^{-1} \text{ K}^{-1}$ ). Again, we utilized the 'DEOPTIM' parameter optimization algorithm in R to fit the temperature response model (Eqn. 4).

$$V_{c,\max,T} = V_{c,\max,25} \exp \left[ \frac{E_a (T_{\text{leaf}} - 298.15)}{(298.15 R T_{\text{leaf}})} \right] \quad \text{Eqn 4}$$

## Biochemical analysis

The leaf area enclosed by the leaf chamber of the IRGA was removed, placed in a paper envelope and dried to a constant mass ( $70^\circ\text{C}$ , Lindberg Blue M, Thermo Scientific, Waltham MA, USA) before shipping to Brookhaven National Laboratory. Leaf samples were weighed to obtain the leaf mass area (LMA,  $\text{g m}^{-2}$ ) and then ground to a fine powder using a ball mill (2000 Geno Grinder; Spex Sample Prep, Cridersville, OH, USA). A 1.50–2.50-mg aliquot was weighed in 0.1-ml tin foil vials (AX26DR; Mettler Toledo, Columbus, OH, USA) and used to determine the C to N ratio ( $\text{CN}_{\text{ratio}}$ ) and elemental N content employing a CHNS/O elemental analyzer operated in CHN mode, according to the manufacturer's instructions (2400 Series II CHNS/O Analyzer; Perkin Elmer, Waltham, MA, USA).

## The fraction of leaf N invested in Rubisco

The fraction of leaf N invested in Rubisco ( $F_{\text{LNR}}$ ) can be calculated as described previously (Thornton & Zimmermann, 2007) following Eqn 5, where leaf N content on an area basis ( $N_a$ ,  $\text{g m}^{-2}$ ) and  $V_{c,\max,25}$  are PFT-specific inputs, and the specific activity of Rubisco ( $\alpha_{\text{R25}}$ ) and the mass ratio of total Rubisco molecular mass to N in Rubisco ( $F_{\text{NR}}$ ) are considered to be global constants.

$$F_{\text{LNR}} = \frac{V_{c,\max,25}}{N_a F_{\text{NR}} \alpha_{\text{R25}}} \quad \text{Eqn 5}$$

We derived  $F_{\text{LNR}}$  from the mean  $V_{c,\max,25}$  (Fig. 2a), mean  $N_a$  (Fig. 4a) and the values for  $F_{\text{NR}}$  ( $6.22 \text{ g Rubisco g}^{-1} \text{ N}$  in Rubisco) and  $\alpha_{\text{R25}}$  ( $47.3 \mu\text{mol CO}_2 \text{ g}^{-1} \text{ Rubisco s}^{-1}$ ) provided by Rogers (2014).



## Models considered

We looked at the model parameterization for all the TBMs represented in the fourth and fifth phases of the Coupled Climate Carbon Cycle Model Intercomparison Project (Friedlingstein *et al.*, 2006, 2014) and those identified in a recent review of global scale models (Smith & Dukes, 2013). Only four models included explicit parameterization of an Arctic PFT and were considered in detail here (Table 1). In order to compare the parameterization of these four models with the data presented in this study and, importantly, to avoid mixing and matching temperature response functions and kinetic constants (Rogers *et al.*, 2017c), we scaled our measured photosynthetic parameters to 25°C using the temperature response functions and  $Q_{10}$  values or activation energies for  $V_{c,max}$  and  $J_{max}$  used by the models (Table 1). For the Atmosphere–Vegetation Interaction Model (AVIM), it was necessary to refit the  $A-C_i$  response curves using the kinetic constants and TRFs employed by Collatz *et al.* (1991), and then scale  $V_{c,max,T}$  to 25°C using the  $Q_{10}$  temperature response function for AVIM presented in Table 1. To account for the temperature acclimation formulations in the Biosphere Energy Transfer Hydrology Scheme (BETHY) and Community Land Model (CLM) used in the calculation of  $JV_{ratio,25}$  and  $\Delta S$  (Table 1), we employed data from a nearby flux tower to provide mean daily air temperature for the proceeding 10 (CLM) and 30 (BETHY) days. For CLM, this 10-d mean temperature was below the restricted temperature range implemented in the model, and therefore the 11°C default value was used in our calculations (Oleson *et al.*, 2013).

## Statistical analysis

Significant ( $P < 0.05$ ) variation among species was identified using a one-way analysis of variance (ANOVA). Significant differences between an individual species (or the seven species mean) and an individual TBM input were identified using a one-sample  $t$ -test. Significant differences between the measured photosynthetic parameters and the model inputs from the four TBMs, and differences between the leaf-level photosynthesis modeled with the measured parameterization and TBM parameterization, were identified using a two-tailed Student's  $t$ -test.

## Results

### Activation energy values associated with the temperature response functions of $V_{c,max}$ and $J_{max}$

Fitting an Arrhenius temperature response function (Eqn 4, Fig. 1) to our full datasets of  $V_{c,max,T}$  and  $J_{max,T}$  showed that the derived  $E_a$  values associated with the temperature response functions of  $V_{c,max}$  and  $J_{max}$  were *c.* 17% lower than the values reported by Bernacchi *et al.* (2001, 2003). If the  $E_a$  values derived by Bernacchi *et al.* (2001) were used to scale model inputs of  $V_{c,max,25}$  and  $J_{max,25}$  values to a typical Arctic growth temperature (5°C),  $V_{c,max}$  and  $J_{max}$  would be underestimated by *c.* 25%. Similarly scaling our measured values to 25°C using our  $E_a$  values would result in a lower  $V_{c,max,25}$  and  $J_{max,25}$  than if those same

values were scaled to 25°C using the TRFs of Bernacchi *et al.* (2001, 2003). Therefore, we used the  $E_a$  values determined in this study (Fig. 1) to scale our data to a common reference temperature of 25°C. Values of  $E_a$  generated from small species-specific datasets, or datasets with a limited temperature range, have the potential to introduce additional sources of uncertainty. Therefore, we adopted the community-level  $E_a$  values presented in Fig. 1 rather than use species-specific  $E_a$  values.

### Photosynthetic traits and key model inputs

Estimates of the key TBM inputs, apparent  $V_{c,max,25}$  and apparent  $J_{max,25}$  (Fig. 2a,b), were determined from  $A-C_i$  response curves made at growth temperature and scaled to 25°C using the temperature response function shown in Eqn 4 and the  $E_a$  values for  $V_{c,max}$  and  $J_{max}$  determined in this study (Fig. 1). These values were used to calculate the apparent  $JV_{ratio}$  at 25°C ( $JV_{ratio,25}$ , Fig. 2c). Apparent mean  $V_{c,max,25}$  (Fig. 2a) showed significant ( $F_{6,173} = 19.2$ ,  $P < 0.001$ ) variation between species, ranging from  $69 \mu\text{mol m}^{-2} \text{s}^{-1}$  in *D. fisheri* to  $113 \mu\text{mol m}^{-2} \text{s}^{-1}$  in *A. fulva*. Apparent  $JV_{ratio,25}$  did not differ significantly between species ( $F_{6,142} = 1.9$ ,  $P = 0.08$ , Fig. 2c), and therefore species variation in apparent  $J_{max,25}$  mirrored apparent  $V_{c,max,25}$ , ranging from  $183 \mu\text{mol m}^{-2} \text{s}^{-1}$  in *D. fisheri* to  $297 \mu\text{mol m}^{-2} \text{s}^{-1}$  in *A. fulva* ( $F_{6,142} = 14.4$ ,  $P < 0.001$ , Fig. 2b). In order to compare the shape of the  $A-C_i$  curves between species that were measured at a range of temperatures, we modeled the response of  $A$  to  $C_i$  at two leaf temperatures (5 and 15°C) using Eqns 1–3 and the mean species-specific values for  $V_{c,max,25}$  and  $J_{max,25}$  presented here (Fig. 2a,b). In all seven species at both 5°C (Fig. 3a) and 15°C (Fig. 3b), photosynthesis was Rubisco limited (RuBP saturated) at current  $[\text{CO}_2]$ . At 5°C, photosynthesis was Rubisco limited throughout the  $A-C_i$  curve. Even at 15°C, photosynthesis did not become RuBP limited in any species until the atmospheric  $\text{CO}_2$  concentration reached *c.*  $785 \mu\text{mol mol}^{-1}$  (a  $C_i$  of *c.*  $550 \mu\text{mol mol}^{-1}$ , Fig. 3b).

Leaf N content ( $N_a$ , Fig. 4a), calculated from the leaf mass area (LMA, Fig. 4b) and mass-based N content ( $N_m$ , data not shown), also varied significantly between species ( $F_{6,151} = 37.6$ ,  $P < 0.001$ ), but did not show the same pattern as  $V_{c,max,25}$  or  $J_{max,25}$ . The LMA and  $\text{CN}_{ratio}$  (Fig. 4c) both varied significantly between species (LMA,  $F_{6,162} = 40.4$ ,  $P < 0.001$ ;  $\text{CN}_{ratio}$ ,  $F_{6,153} = 64$ ,  $P < 0.001$ ). Our paired gas exchange and  $N_a$  dataset allowed us to calculate  $F_{LNR}$  (Fig. 5), which varied significantly between species ( $F_{6,156} = 80$ ,  $P < 0.001$ ) and was notably high in *A. fulva*, where 34% of leaf N was invested in Rubisco.

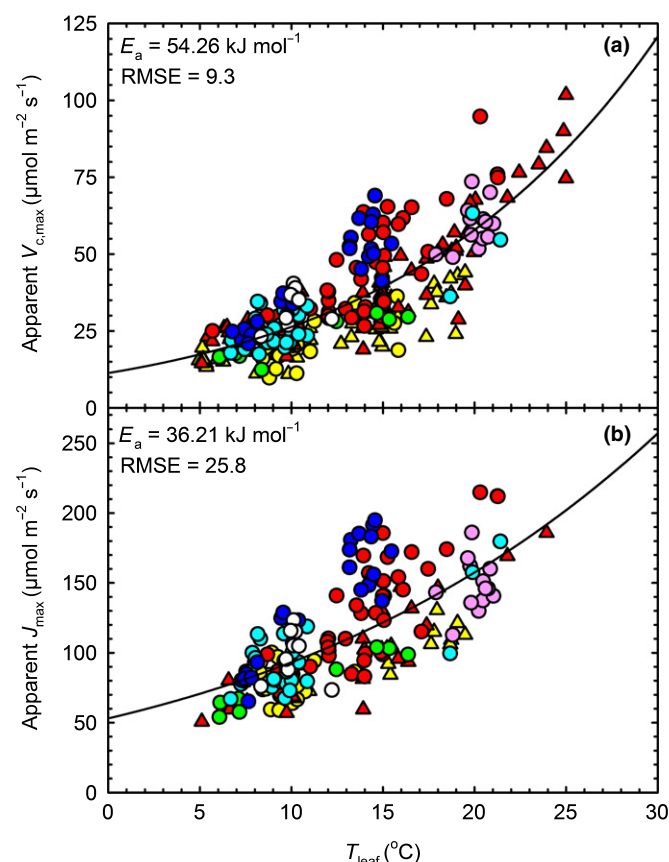
### $V_{c,max}$ –leaf N relationship

We found no clear relationship between apparent  $V_{c,max,25}$  and  $N_a$  (Fig. 6). We doubled the size of our  $V_{c,max}-N_a$  dataset by leveraging estimates of apparent  $V_{c,max,25}$  derived from an additional dataset of light-saturated  $A$  ( $A_{sat}$ ) using the one-point method for the estimation of  $V_{c,max,25}$  (De Kauwe *et al.*, 2016) and coupled measurements of  $N_m$  and LMA. When we included the derived apparent  $V_{c,max,25}$  and  $N_a$  data in our analysis, we

**Table 1** Parameters and equations used by the four terrestrial biosphere models (TBMs) that include an Arctic plant functional type (PFT); the Atmosphere–Vegetation Interaction Model (AVIM), the Biosphere Energy Transfer Hydrology Scheme (BETHY), the Community Land Model v4.5 (CLM4.5) and Hybrid version 6.5 (Hybrid6.5)

	AVIM	BETHY	CLM4.5	Hybrid6.5
Form of FvCB model	$A = (A_c, A_i) - R_d$ Collatz <i>et al.</i> (1991)	$A = (A_c, A_i) - R_d$	$A = (A_c, A_i, A_p) - R_d$	$A = (A_c, A_i) - R_d$ Kull & Kruijt (1998)
$V_{c,max,25}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	55	20	78	37
Temperature acclimation of $J_{V_{ratio,25}}$ (source)	NA	In CLM, acclimation to low temperature is restricted where $(T_g - T_l) \geq 11^\circ\text{K}$ Kattge & Knorr (2007)	$J_{V_{ratio,25}} = 2.59 - 0.035(T_g - T_l)$ where $(T_g - T_l) \geq 11^\circ\text{K}$ Kattge & Knorr (2007)	NA
$J_{V_{ratio,25},T_g}$	NA	2.44	2.21	NA
$J_{max,25}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	NA	49	172	209*
Source of kinetic constants	Collatz <i>et al.</i> (1991)	Bernacchi <i>et al.</i> (2001, 2003), Kattge & Knorr (2007)	Bernacchi <i>et al.</i> (2001, 2003), Kattge & Knorr (2007)	Bernacchi <i>et al.</i> (2001), Friend (1995)
Temperature response functions	$V_{c,max} = V_{c,max,25} Q_{10}^{\frac{(T_{leaf}-25)}{10}}$	$V_{c,max} = V_{c,max,25} \exp\left(E_a \frac{T_{leaf}-298.15}{298.15R T_{leaf}}\right)$ $\Delta S = 668.39 - 1.07(T_g - T_l)$ In CLM, acclimation to low temperature is restricted where $(T_g - T_l) \geq 11$ Kattge & Knorr (2007)	$V_{c,max} = V_{c,max,25} \exp\left(E_a \frac{T_{leaf}-298.15}{298.15R T_{leaf}}\right)$ $\Delta S = 668.39 - 1.07(T_g - T_l)$ In CLM, acclimation to low temperature is restricted where $(T_g - T_l) \geq 11$ Kattge & Knorr (2007)	$V_{c,max} = \exp\left(\frac{C-E_a}{R T_{leaf}}\right)$ $j_{max} = \frac{\alpha_T \exp\left(\frac{-E_d}{R T_{leaf}}\right)}{1 + \exp\left[\frac{(\Delta S T_{leaf} - E_d)}{R T_{leaf}}\right]}$
Temperature response parameters for $V_{c,max}$	$Q_{10} = 2.4$	$E_a = 71.510 \text{ kJ mol}^{-1}$ $E_d = 200 \text{ kJ mol}^{-1}$ $\Delta S = 650 \text{ J K}^{-1} \text{ mol}^{-1}$	$E_a = 72 \text{ kJ mol}^{-1}$ $E_d = 200 \text{ kJ mol}^{-1}$	$E_a = 65.33 \text{ kJ mol}^{-1}$ $c = 26.35$
Temperature response parameters for $J_{max}$	NA	NA	NA	$\alpha_T = 3.486 \times 10^{13} \text{ mol mol}^{-1} \text{s}^{-1}$ $E_a = 79.5 \text{ kJ mol}^{-1}$ $E_d = 199 \text{ kJ mol}^{-1}$ $\Delta S = 650 \text{ J K}^{-1} \text{ mol}^{-1}$
$CN_{ratio}$	NA	NA	25	NA
$N_a$ ( $\text{g m}^{-2}$ )	NA	NA	1.3	1.6
Apparent $F_{LNR}$	NA	NA	0.1365	0.078
Key model reference	Lu & Ji (2006)	Ziehn <i>et al.</i> (2011)	Oleson <i>et al.</i> (2013)	Friend & Kiang (2005)

A,  $\text{CO}_2$  assimilation rate;  $A_p$ , RuBP saturated  $\text{CO}_2$  assimilation rate;  $A_i$ , RuBP limited  $\text{CO}_2$  assimilation rate;  $A_p$ , triose phosphate export limited rate of  $\text{CO}_2$  assimilation;  $T_g$ , the preceding 10 d (CLM, 4.25°C) and 30 d (BETHY, 4.28°C) mean air temperature ( $^\circ\text{K}$ ) calculated in this study from data from a nearby flux tower (Torn *et al.*, 2014);  $T_l$ , freezing point of water ( $^\circ\text{K}$ );  $J_{V_{ratio,25}}$ ,  $J_{V_{ratio,25}}$  acclimated to growth temperature;  $E_a$ , activation energy;  $E_d$ , deactivation energy;  $R$ , universal gas constant;  $\Delta S$ , entropy factor;  $j_{max}$ , light saturated potential electron transport (mole electrons  $\text{mol}^{-1}$  chlorophyll  $\text{s}^{-1}$ ) rate;  $\alpha_T$ , a constant linking electron to chlorophyll content. \* $J_{max}$  was calculated from  $j_{max}$  as described previously (Friend, 1995). Apparent  $F_{LNR}$  for Hybrid6.5 was calculated from  $N_a$  and  $V_{c,max,25}$  based on Rogers (2014). NA, not applicable.

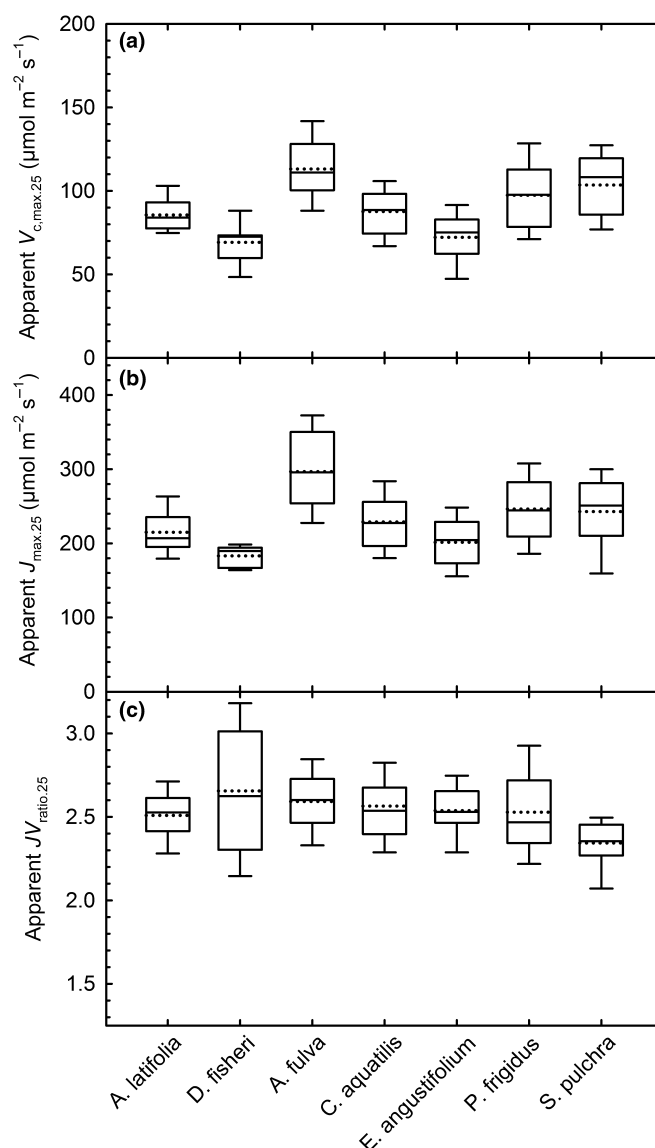


**Fig. 1** Apparent maximum carboxylation rate ( $V_{c,max}$ , a) and apparent maximum electron transport rate ( $J_{max}$ , b) measured on individual ramets at ambient growth temperature (circles, seven species) and at multiple leaf temperatures on the same ramet (upward pointing triangles, two species) in *Arctagrostis latifolia* (pink), *Dupontia fisheri* (green), *Arctophila fulva* (blue), *Carex aquatilis* (cyan), *Eriophorum angustifolium* (yellow), *Petasites frigidus* (red) and *Salix pulchra* (white) growing on the Barrow Environmental Observatory, Barrow, Alaska. An Arrhenius temperature response (black line) was fitted to the data in order to calculate an activation energy ( $E_a$ ) for both  $V_{c,max}$  and  $J_{max}$ .

still found that  $N_a$  could explain no more than 2% of the variation in  $V_{c,max,25}$  (Fig. 6).

### Comparison with TBM parameterization

To enable fair comparison of the gas exchange data presented here with the model parameterization in the four TBMs considered, we scaled our data from growth temperature to 25°C using model-specific temperature response functions and parameterization (Table 1). All four models markedly and significantly (one-sample  $t$ -tests,  $P < 0.05$ ) underestimated  $V_{c,max,25}$  in all seven species (Fig. 7), ranging from CLM (Fig. 7c, long dashes), where the model parameterization was 42% lower than the seven species mean, to BETHY (Fig. 7b), where the model parameterization was five times lower than the seven species mean. The model comparison with measured  $J_{max,25}$  (Fig. 8) shows that, for BETHY (Fig. 8a) and CLM (Fig. 8b),  $J_{max,25}$  was markedly and significantly higher than the model parameterization: 55% higher in CLM (Fig. 8b) and over five-fold higher in BETHY (Fig. 8a;



**Fig. 2** Apparent maximum carboxylation rate ( $V_{c,max,25}$ , a) and apparent maximum electron transport rate ( $J_{max,25}$ , b) scaled to 25°C using the  $E_a$  values determined from the temperature response of  $V_{c,max}$  and  $J_{max}$  presented in Fig. 1, and the ratio of  $J_{max,25}$  to  $V_{c,max,25}$  ( $JV_{ratio,25}$ , c). Data were measured in seven species located on the Barrow Environmental Observatory, Barrow, Alaska. All data presented in this figure were derived from measurements made at ambient temperature. Box plots show the interquartile range (box), median (solid line) and mean (broken line). The whiskers show the lowest and highest datum still within  $1.5 \times$  interquartile range of the lower and upper quartiles ( $n = 8\text{--}44$  plants).

Table 1). In TBMs,  $J_{max,25}$  is typically calculated from the model estimate of  $V_{c,max,25}$  and  $JV_{ratio,25}$ . The species mean  $JV_{ratio,25}$  ( $2.53 \pm 0.04$  SE, Fig. 2c) is 4% and 13% higher than  $JV_{ratio,25}$  used by BETHY (2.44) and CLM (2.21), respectively (one-sample  $t$ -tests,  $P < 0.05$ , Fig. 2c, Table 1). The use of our Arctic  $E_a$  values resulted in a small ( $c. 10\%$ ), but significant ( $t_{(6)} = 8.1$ ,  $P < 0.001$ ), increase in the observed  $JV_{ratio,25}$  when compared with the  $JV_{ratio,25}$  that would have been obtained using the  $E_a$  values provided by Bernacchi *et al.* (2001, 2003). The Hybrid model uses a different approach to estimate  $J_{max,25}$  based on  $N_a$

(Table 1); as a result, the pattern of derived  $J_{\max,25}$  for Hybrid follows that of  $N_a$  (Fig. 4a). The Hybrid  $J_{\max,25}$  estimate was significantly higher than *A. latifolia*, *D. fisheri* and *A. fulva*, but significantly lower than *C. aquatilis*, *E. angustifolium*, *P. frigidus* and *S. pulchra* (one-sample  $t$ -tests,  $P < 0.05$ ).

Model parameterization associated with leaf chemistry more closely matched the observations. For  $N_a$ , the seven-species mean was not significantly different from the value used by Hybrid (Fig. 4a, short dashes), but was significantly (one-sample  $t_{(6)} = 2.1$ ,  $P < 0.05$ ) higher than the mean used by CLM (Fig. 4a, long dashes). CLM also uses  $CN_{\text{ratio}}$  as a model input and the seven-species mean was 23% lower than the CLM value (one-sample  $t_{(6)} = 2.4$ ,  $P > 0.05$ ). With the exception of *E. angustifolium*, all species had a higher investment in Rubisco than that prescribed by CLM, and the seven-species mean was  $\approx 30\%$  higher than the model input (one sample  $t_{(6)} = 2.1$ ,  $P < 0.05$ , Fig. 5, long dashed line). The  $F_{\text{LNR}}$  value calculated for Hybrid was 60% lower than the observed seven-species mean (Fig. 5, short dashed line).

### Comparison of modeled and measured CO<sub>2</sub> assimilation

To evaluate the effect of these new data on the modeled CO<sub>2</sub> uptake in the Arctic, we compared model estimates for light-saturated leaf-level  $A$  at 5°C modeled with the TBM-specific parameterization and TRFs (Table 1) with the data presented here (Figs 1, 2). The mean observed  $V_{c,\max,5}$  was more than twice the TBM model mean  $V_{c,\max,5}$  ( $t_{(5)} = 4.6$ ,  $P < 0.01$ , Table 2), and the resulting species mean  $A$  modeled using our parameterization and TRF was 2.5 times greater than the  $A$  value modeled with current TBM parameterization ( $t_{(5)} = 4.6$ ,  $P < 0.01$ , Table 2).

As an additional step, we compared our modeled data with independent measurements of light-saturated  $A$  made in the field at 5°C in 2016. These data showed that  $A$  modeled with the mean TBM parameterization of  $V_{c,\max,25}$  resulted in a CO<sub>2</sub> uptake rate that was less than half the measured CO<sub>2</sub> assimilation rate ( $t_{(3)} = 3.7$ ,  $P < 0.05$ ).  $A$  modeled with the parameter values

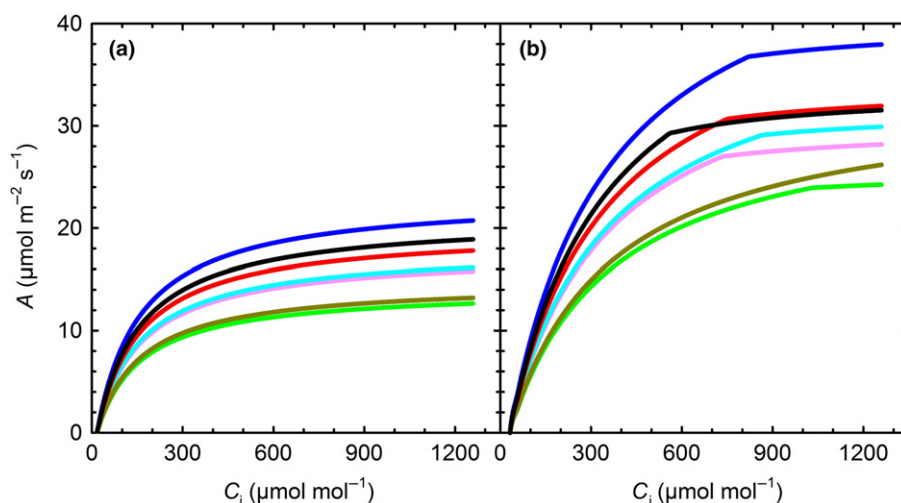
determined by this study was  $\approx 20\%$  higher than the measured values, but not significantly different ( $t_{(9)} = 2.2$ ,  $P > 0.05$ ) from  $A$  measured in 2016.

### Discussion

We have shown that TBM representation of photosynthetic capacity in Arctic vegetation markedly underestimates the capacity for CO<sub>2</sub> assimilation in this globally important biome. Our data showed that the photosynthetic capacity was high (Fig. 2) – all seven species had values for  $V_{c,\max,25}$  that were comparable with, or higher than, those found in major C3 crops (Bernacchi *et al.*, 2005; James *et al.*, 2006; Zhu *et al.*, 2012) – and up to five times higher than some model estimates (Fig. 7). Leaf-level modeling demonstrated that current TBM parameterization of photosynthetic capacity results in a two-fold underestimation of CO<sub>2</sub> assimilation by Arctic vegetation (Table 2). This study provides one of the first datasets of the key photosynthetic parameters  $V_{c,\max}$  and  $J_{\max}$  in Arctic vegetation and the first estimates of their TRFs (Figs 1, 2). Our data also showed that model underestimation of photosynthetic capacity is attributable to a combination of low estimates of the leaf N content (Fig. 4) and the fraction of N partitioned to Rubisco (Fig. 5).

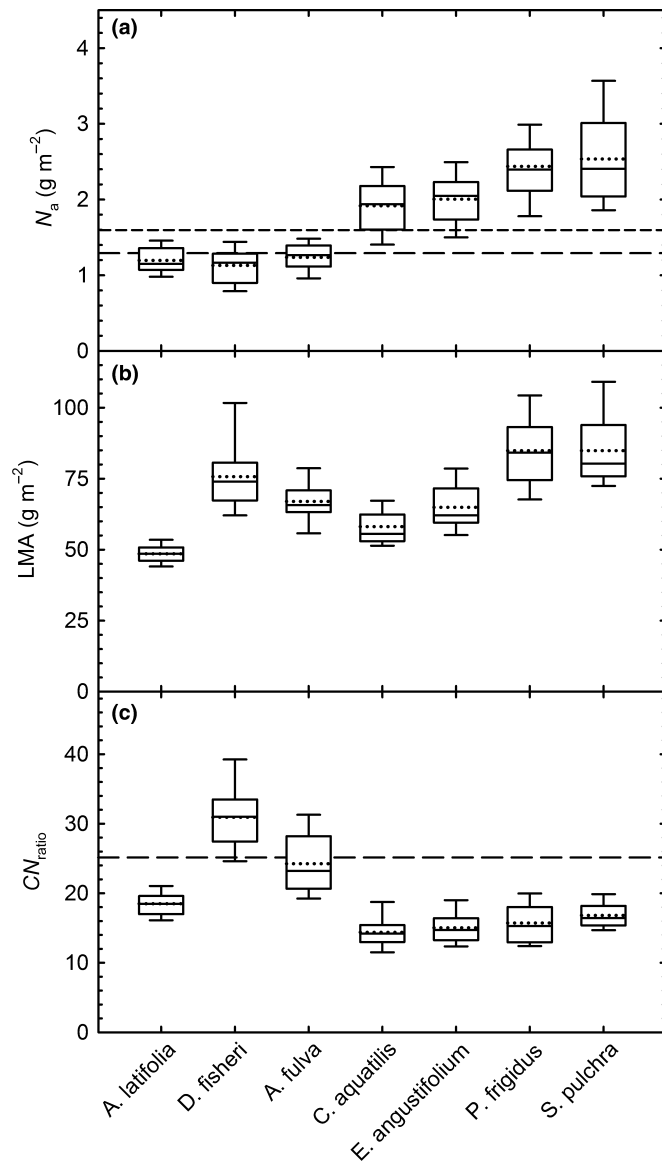
The  $JV_{\text{ratio}}$  affects the CO<sub>2</sub> responsiveness of  $A$ , such that a high  $JV_{\text{ratio}}$  will mean that  $A$  remains RuBP saturated at a high [CO<sub>2</sub>], and is therefore more responsive to increasing [CO<sub>2</sub>], than RuBP limited  $A$  in a plant with a lower  $JV_{\text{ratio}}$  (Rogers *et al.*, 2017c). The result of the high  $JV_{\text{ratio}}$  in these Arctic species can be readily seen in Fig. 3b, where, even at 15°C,  $A$  does not become RuBP limited in any species until a  $C_i$  value of  $\approx 550 \mu\text{mol mol}^{-1}$ . This means that Arctic vegetation has the potential to respond maximally to rising [CO<sub>2</sub>] through most of this century. The high investment in Rubisco, coupled with the high  $JV_{\text{ratio},25}$ , enables plants growing at current [CO<sub>2</sub>] to sustain high, RuBP-saturated, photosynthetic rates, even at low temperature and low light levels.

The high  $JV_{\text{ratio}}$  will also enable Arctic plants to continue CO<sub>2</sub> assimilation during the continuous but lower irradiance of the



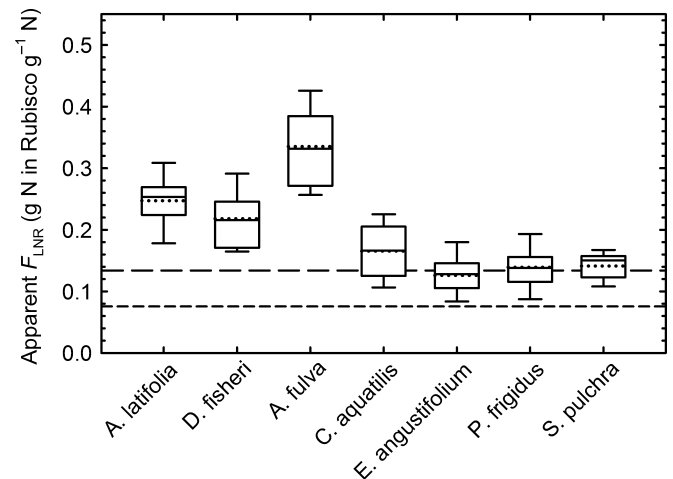
**Fig. 3** Synthetic  $A$ – $C_i$  curves modeled at 5°C (a) and 15°C (b). The response of photosynthesis ( $A$ ) to rising intercellular CO<sub>2</sub> concentration ( $C_i$ ) was modeled based on the data presented in Figs 1 and 2 and Eqns 1–3 for the seven species considered in this study: *Arctagrostis latifolia* (pink), *Dupontia fisheri* (green), *Arctophila fulva* (blue), *Carex aquatilis* (cyan), *Eriophorum angustifolium* (dark yellow), *Petasites frigidus* (red) and *Salix pulchra* (black).



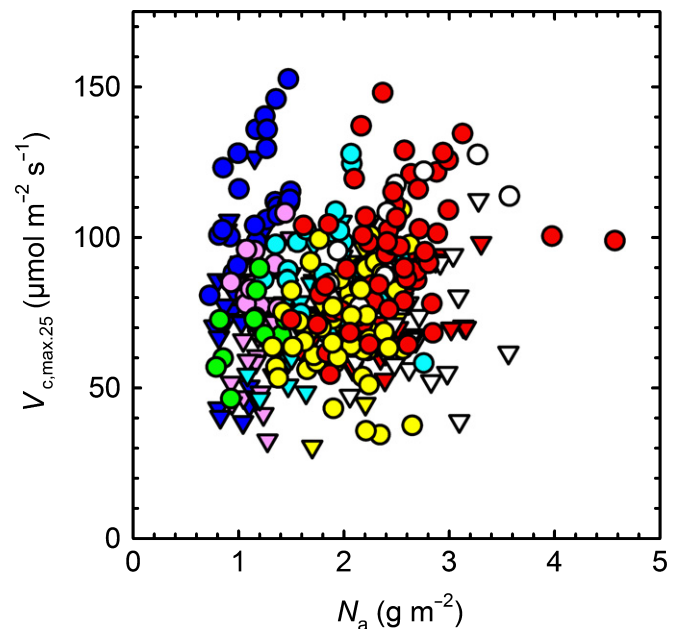


**Fig. 4** Leaf nitrogen content ( $N_a$ ,  $\text{g m}^{-2}$ , a), leaf mass area (LMA,  $\text{g m}^{-2}$ , b) and the ratio of leaf carbon to nitrogen content ( $\text{CN}_{\text{ratio}}$ , c). Data were collected in parallel with gas exchange in seven species located on the Barrow Environmental Observatory, Barrow Alaska. The broken lines in (a) indicate the mean value of  $N_a$  used by the Hybrid (short dashes) and Community Land Model (CLM) (long dashes) to parameterize the Arctic plant functional type (PFT). The broken line in (c) indicates the  $\text{CN}_{\text{ratio}}$  used by CLM to parameterize the Arctic PFT. Box plots show the interquartile range (box), median (solid line) and mean (broken line). The whiskers show the lowest and highest datum still within  $1.5 \times$  interquartile range of the lower and upper quartiles ( $n = 8\text{--}44$  plants).

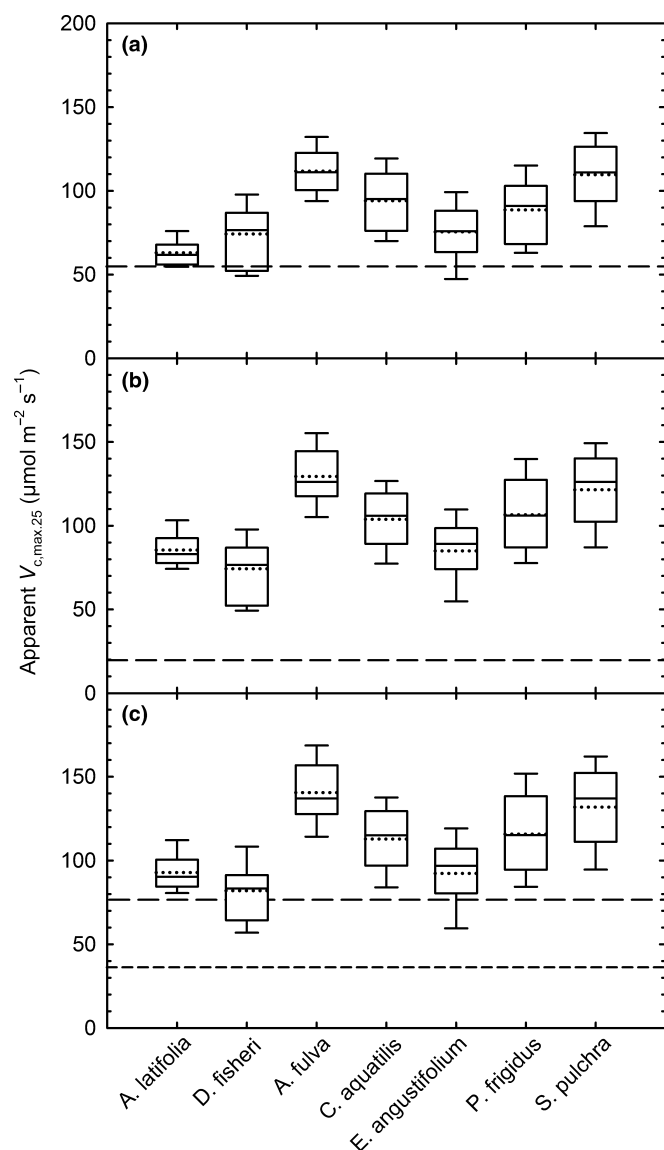
Arctic midnight sun, and also to maximally exploit periods of high light on clear days during the short Arctic thaw season. In addition, many Arctic plants emerge from underneath the snow at the beginning of the growth season where temperatures are low, light levels are low and  $[\text{CO}_2]$  is typically elevated (Starr & Oberbauer, 2003; Saarinen *et al.*, 2016). Plants with a high investment in Rubisco and a high  $JV_{\text{ratio}}$  would be well adapted to exploit such conditions.



**Fig. 5** The apparent fraction of leaf nitrogen invested in Rubisco ( $F_{\text{LNR}}$ ) calculated using Eqn 5 from the data provided in Figs 2 and 4 and Rogers (2014). The broken lines show the value of  $F_{\text{LNR}}$  used in the Community Land Model (CLM) to parameterize the Arctic plant functional type (PFT, long dashes) and the  $F_{\text{LNR}}$  calculated for Hybrid based on  $N_a$  and  $V_{c,\text{max},25}$  in Table 1 (short dashes). Box plots show the interquartile range (box), median (solid line) and mean (broken line). The whiskers show the lowest and highest datum still within  $1.5 \times$  interquartile range of the lower and upper quartiles ( $n = 8\text{--}44$  plants).

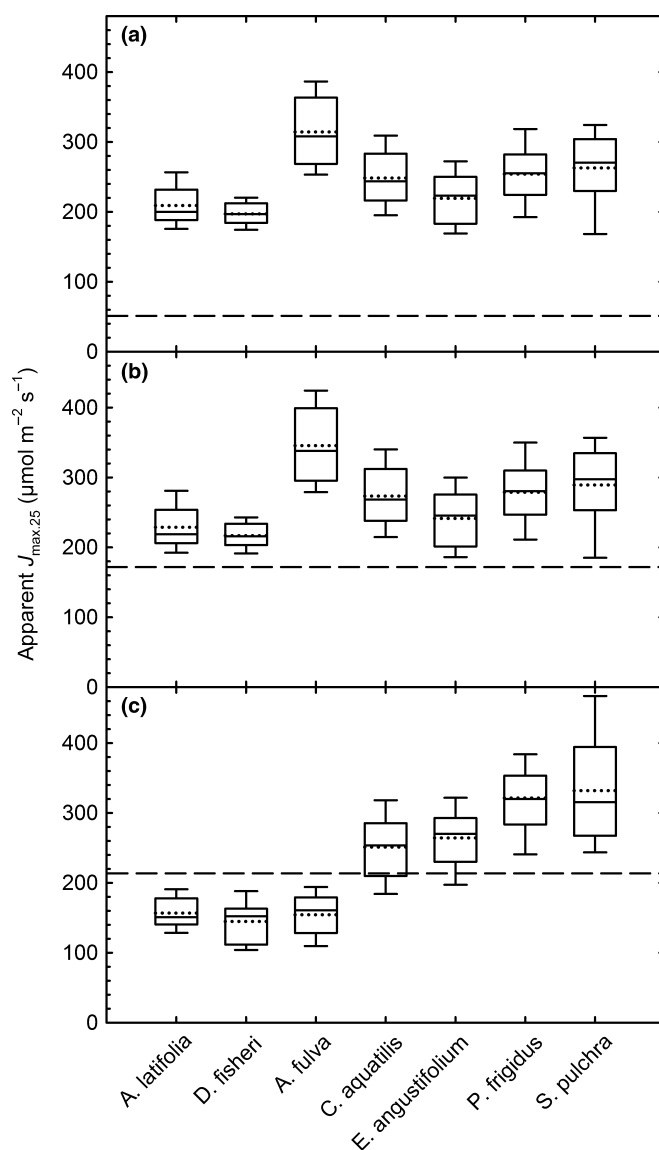


**Fig. 6** Apparent maximum carboxylation rate scaled to  $25^\circ\text{C}$  ( $V_{c,\text{max},25}$ ) plotted against the area-based leaf nitrogen content ( $N_a$ ). Estimates of apparent  $V_{c,\text{max},25}$  were scaled from gas exchange measurements made at growth temperature. These estimates were derived from A–C<sub>i</sub> curves (circles) made between 2012 and 2015, and from steady-state, light-saturated photosynthesis using the one-point method made in 2016 (downward pointing triangles). Measurements were made on individual ramets of *Arctagrostis latifolia* (pink), *Dupontia fisheri* (green), *Arctophila fulva* (blue), *Carex aquatilis* (cyan), *Eriophorum angustifolium* (yellow), *Petasites frigidus* (red) and *Salix pulchra* (white) growing on the Barrow Environmental Observatory, Barrow, Alaska. No significant correlation was found.



**Fig. 7** Apparent maximum carboxylation rate measured at growth temperature and scaled to 25°C (apparent  $V_{c,max,25}$ ) using the temperature response functions and parameterization associated with the four terrestrial biosphere models (TBMs) considered in this study (Table 1). The TBM model inputs are shown with a broken line: Atmosphere–Vegetation Interaction Model (AVIM) (a), Biosphere Energy Transfer Hydrology Scheme (BETHY) (b), Community Land Model (CLM) (long dashes, c) and Hybrid (short dashes, c). Gas exchange was measured in seven species located on the Barrow Environmental Observatory, Barrow, Alaska. Box plots show the interquartile range (box), median (solid line) and mean (broken line). The whiskers show the lowest and highest datum still within  $1.5 \times$  interquartile range of the lower and upper quartiles ( $n = 8–44$  plants).

We observed a  $JV_{ratio,25}$  (2.53) that is 28% higher than the  $JV_{ratio,25}$  used by many models which do not account for temperature acclimation of photosynthesis (e.g. 1.97, Bonan *et al.*, 2011), highlighting the need for TBMs to account for thermal acclimation. Kattge & Knorr (2007) developed an approach to account for the acclimation of  $JV_{ratio,25}$  to growth temperature, but their work did not include any measurements at which the growth temperature was below 10°C, and the data from boreal



**Fig. 8** Apparent maximum electron transport rate measured at growth temperature and scaled to 25°C (apparent  $J_{max,25}$ ) using the temperature response functions, parameterization or the relationship with  $N_a$  (Hybrid), associated with three of the four terrestrial biosphere models (TBMs: Biosphere Energy Transfer Hydrology Scheme (BETHY), a; Community Land Model (CLM), b; Hybrid, c) considered in this study. The broken lines with long dashes in each panel indicate the TBM parameterization for the Arctic plant functional type (PFT). Gas exchange was measured in seven species located on the Barrow Environmental Observatory, Barrow, Alaska. Box plots show the interquartile range (box), median (solid line) and mean (broken line). The whiskers show the lowest and highest datum still within  $1.5 \times$  interquartile range of the lower and upper quartiles ( $n = 8–44$  plants).

species in their study appeared to be outliers, exhibiting a markedly lower  $JV_{ratio,25}$  than other species. This study adds new data at the low-temperature end of the synthesis by Kattge & Knorr (2007) and supports the relationship they presented, which is implemented in BETHY and CLM. However, the  $JV_{ratio,25}$  observed here was still markedly higher than the value used in CLM, because CLM includes a lower limit for growth temperature of 11°C. This study suggests that, to more accurately

**Table 2** Modeled and measured light-saturated CO<sub>2</sub> assimilation at 5°C

Species/TBM	Modeled photosynthesis		Measured photosynthesis A (μmol m <sup>-2</sup> s <sup>-1</sup> )
	V <sub>c,max,5</sub> (μmol m <sup>-2</sup> s <sup>-1</sup> )	A (μmol m <sup>-2</sup> s <sup>-1</sup> )	
<i>Arctagrostis latifolia</i>	17.9	11.2	9.2 ± 2.5
<i>Dupontia fisheri</i>	14.4	9.0	ND
<i>Arctophila fulva</i>	23.5	14.8	10.1 ± 1.8
<i>Carex aquatilis</i>	18.3	11.5	8.8 ± 1.9
<i>Eriophorum angustifolium</i>	15.0	9.4	10.1 ± 1.6
<i>Petasites frigidus</i>	20.2	12.7	11.3 ± 2.7
<i>Salix pulchra</i>	21.4	13.5	9.1 ± 2.5
<b>Species mean</b>	<b>18.6 ± 3.3</b>	<b>11.7 ± 2.1</b>	<b>9.8 ± 0.9</b>
AVIM	9.5	6.0	
BETHY	2.0	1.3	
CLM4.5	11.8	7.4	
Hybrid6.5	5.6	3.5	
<b>Model mean</b>	<b>7.2 ± 4.3</b>	<b>4.5 ± 2.7</b>	

Leaf-level CO<sub>2</sub> assimilation (A) modeled for the seven Arctic species in this study and for the Arctic plant functional types (PFT) represented in four terrestrial biosphere models (Table 1). Leaf-level, light-saturated A was modeled using Eqns 1–3, where leaf temperature = 5°C, CO<sub>2</sub> concentration = 390 μmol mol<sup>-1</sup>, O<sub>2</sub> concentration = 210 mmol mol<sup>-1</sup> and C<sub>i</sub> : C<sub>a</sub> ratio = 0.7. Under these conditions, photosynthesis was limited by carboxylation capacity. V<sub>c,max,5</sub> for the seven species was obtained by scaling V<sub>c,max,25</sub> (Fig. 2) to 5°C using Eqn 4 and the E<sub>a</sub> values presented in Fig. 1. V<sub>c,max,5</sub> for the models was calculated by scaling V<sub>c,max,25</sub> for the Arctic PFT using the model-specific V<sub>c,max,25</sub> and temperature response function (TRF) (Table 1). Measured photosynthesis (n = 8–17 individual ramets per species, ± SD) was derived from a separate study on different plants in different locations on the Barrow Environmental Observatory (BEO), measured in a different year, where mean T<sub>leaf</sub> = 5°C. Species and model means are shown ± SD. AVIM, Atmosphere–Vegetation Interaction Model; BETHY, Biosphere Energy Transfer Hydrology Scheme; CLM4.5, Community Land Model v.4.5; Hybrid6.5, Hybrid v.6.5; ND, no data; TBM, terrestrial biosphere model.

capture the J<sub>V<sub>ratio,25</sub></sub> in Arctic species, this lower limit should be removed from the model formulation.

Our biochemical data revealed markedly different strategies for N partitioning in these seven Arctic species. Some species (*A. latifolia*, *D. fisheri* and *A. fulva*) had a tightly constrained N<sub>a</sub>, whereas others, notably *S. pulchra* and *P. frigidus*, had a large range in N<sub>a</sub> (Fig. 4), suggesting that N<sub>a</sub> may drive the greater plasticity in photosynthetic capacity (Fig. 2). Most of the species had a low CN<sub>ratio</sub> in comparison with the value used by CLM (Fig. 4c). This indicates that the high N<sub>a</sub> in some Arctic species is caused, in part, by a higher investment in N per unit C, and not just a high N density per unit leaf area (Fig. 4). Our dataset afforded the opportunity to calculate apparent F<sub>LNR</sub> for these Arctic species (a key model input for CLM), thus providing models with a parameter associated with N partitioning that could be used as a PFT-specific model input, or to evaluate prognostic N allocation models, e.g. Ali *et al.* (2016). It is notable that species with a lower N<sub>a</sub> (*A. latifolia*, *D. fisheri* and *A. fulva*, Fig. 4) also had a high F<sub>LNR</sub> (Fig. 5), suggesting that the high partitioning of N to Rubisco in these species enabled them to produce leaves with a lower N<sub>a</sub> (Fig. 4), but comparable photosynthetic capacity (Fig. 2), which, at the whole-plant level, may enable a higher productivity for a given N supply.

One approach used by TBMs to derive V<sub>c,max,25</sub> is to use PFT-specific slopes and intercepts from the linear relationship with N<sub>a</sub> (Medlyn *et al.*, 1999; Kattge *et al.*, 2009; Walker *et al.*, 2014). Previously, there was insufficient data to examine this relationship in Arctic species (Kattge *et al.*, 2009; Ziehn *et al.*, 2011). We did not observe a V<sub>c,max,25</sub>–N<sub>a</sub> relationship (Fig. 6). The different N allocation strategies outlined above,

and the high diversity of leaf morphology in these species, may explain why we did not observe a V<sub>c,max,25</sub>–N<sub>a</sub> relationship at our field site, a finding also observed in *Betula nana* and *Eriophorum vaginatum* (van der Weg *et al.* 2013). Although data at the global or biome scale often demonstrate a strong relationship between V<sub>c,max,25</sub> and N<sub>a</sub> (Kattge *et al.*, 2009; Walker *et al.*, 2014), these relationships can change markedly and even fall apart at finer scales (Feng & Dietze, 2013; Bahar *et al.*, 2016; Croft *et al.*, 2017), which has led to the use of other variables, including phosphorus, to explain global variation in V<sub>c,max,25</sub> (Walker *et al.*, 2014; Ali *et al.*, 2015; Croft *et al.*, 2017). There is evidence that phosphorus plays a role in limiting the productivity of Arctic tundra ecosystems, and may be a limiting nutrient on the coastal tundra in Barrow (Chapin *et al.*, 1975, 1995; Shaver & Chapin, 1980). However, the examination of N:phosphorus ratios across major biomes suggests that direct phosphorus limitation of photosynthesis in the Arctic is unlikely (Reich *et al.*, 2009).

As recently pointed out, it is critically important for models to make consistent use of kinetic constants and temperature response functions (Rogers *et al.*, 2017c). Therefore, the data presented here should be used in conjunction with the kinetic constants and temperature response functions associated with K<sub>c</sub>, K<sub>o</sub> and Γ\* that are provided by Bernacchi *et al.* (2001). Similarly, use of the Arctic V<sub>c,max,25</sub> and J<sub>max,25</sub> data (Fig. 2) will require temperature scaling with the E<sub>a</sub> values and the TRFs presented here (Fig. 1, Eqn 4). We also recognize that there are many alternative approaches to the analysis of photosynthetic CO<sub>2</sub> response curves, including, for example, those that use different TRFs, correct data for potential chamber leaks or account for mesophyll

conductance (Ethier & Livingston, 2004; Flexas *et al.*, 2007; Sharkey *et al.*, 2007; Gu *et al.*, 2010; Bernacchi *et al.*, 2013). To allow for future reanalysis of our data, and to maximize their further use by the modeling community, all of our data – including our raw gas exchange data – are available online (Rogers *et al.*, 2017a,b). In addition, we have submitted calculated photosynthetic parameters and biochemical trait data to the TRY database (Kattge *et al.*, 2011) and the database (www.BETYdb.org) associated with the Predictive Ecosystem Analyzer (PEcAn) project (Lebauer *et al.*, 2013).

In addition to advancing our understanding of photosynthesis in the Arctic, these data clearly indicate that CO<sub>2</sub> assimilation in Arctic vegetation is poorly represented by current TBMs. Although we caution that these data and insights are only from one site in the high Arctic, this study represents a significant advance, and we hope that the TBM community will improve the representation of CO<sub>2</sub> assimilation in the Arctic by using these data.

## Acknowledgements

We are grateful for the technical assistance provided by Stefanie Lasota. This work was supported by the Next-Generation Ecosystem Experiments (NGEE Arctic) project which is supported by the Office of Biological and Environmental Research in the Department of Energy, Office of Science, and through the United States Department of Energy contract no. DE-SC0012704 to Brookhaven National Laboratory. The authors are grateful to UIC Science for logistical support.

## Author contributions

A.R. designed the study with input from V.L.S., S.P.S. and S.D.W. The data were collected and analyzed by A.R., K.S.E. and S.P.S. The initial draft of the manuscript was prepared by A.R. All authors contributed to the writing.

## References

- Ainsworth EA, Davey PA, Hymus GJ, Osborne CP, Rogers A, Blum H, Nosberger J, Long SP. 2003. Is stimulation of leaf photosynthesis by elevated carbon dioxide concentration maintained in the long term? A test with *Lolium perenne* grown for 10 years at two nitrogen fertilization levels under Free Air CO<sub>2</sub> Enrichment (FACE). *Plant, Cell & Environment* 26: 705–714.
- Albert KR, Mikkelsen TN, Ro-Poulsen H, Arndal MF, Michelsen A. 2011. Ambient UV-B radiation reduces PSII performance and net photosynthesis in high Arctic *Salix arctica*. *Environmental and Experimental Botany* 73: 10–18.
- Ali AA, Xu C, Rogers A, Fisher RA, Wullschlegel SD, Massoud EC, Vrugt JA, Muss JD, McDowell NG, Fisher JB *et al.* 2016. A global scale mechanistic model of photosynthetic capacity (LUNA V1.0). *Geoscientific Model Development* 9: 587–606.
- Ali AA, Xu CG, Rogers A, McDowell NG, Medlyn BE, Fisher RA, Wullschlegel SD, Reich PB, Vrugt JA, Bauerle WL *et al.* 2015. Global-scale environmental control of plant photosynthetic capacity. *Ecological Applications* 25: 2349–2365.
- Alton PB. 2017. Retrieval of seasonal Rubisco-limited photosynthetic capacity at global FLUXNET sites from hyperspectral satellite remote sensing: impact on carbon modelling. *Agricultural and Forest Meteorology* 232: 74–88.
- Ardia D. 2009. *DEoptim: differential evolution optimization in R*. R package, version 1.3-3. <http://CRAN.R-project.org/package=DEoptim>.
- Bahar NHA, Ishida FY, Weerasinghe LK, Guerrieri R, O'Sullivan OS, Bloomfield KJ, Asner GP, Martin RE, Lloyd J, Malhi Y *et al.* 2016. Leaf-level photosynthetic capacity in lowland Amazonian and high-elevation Andean tropical moist forests of Peru. *New Phytologist* 214: 1002–1018.
- Bernacchi CJ, Bagley JE, Serbin SP, Ruiz-Vera UM, Rosenthal DM, Vanloocke A. 2013. Modelling C<sub>3</sub> photosynthesis from the chloroplast to the ecosystem. *Plant, Cell & Environment* 36: 1641–1657.
- Bernacchi CJ, Leakey ADB, Heady LE, Morgan PB, Dohleman FG, McGrath JM, Gillespie KM, Wittig VE, Rogers A, Long SP *et al.* 2006. Hourly and seasonal variation in photosynthesis and stomatal conductance of soybean grown at future CO<sub>2</sub> and ozone concentrations for 3 years under fully open-air field conditions. *Plant, Cell & Environment* 29: 2077–2090.
- Bernacchi CJ, Morgan PB, Ort DR, Long SP. 2005. The growth of soybean under free air CO<sub>2</sub> enrichment (FACE) stimulates photosynthesis while decreasing *in vivo* Rubisco capacity. *Planta* 220: 434–446.
- Bernacchi CJ, Pimentel C, Long SP. 2003. *In vivo* temperature response functions of parameters required to model RuBP-limited photosynthesis. *Plant Cell and Environment* 26: 1419–1430.
- Bernacchi CJ, Singaas EL, Pimentel C, Portis AR, Long SP. 2001. Improved temperature response functions for models of Rubisco-limited photosynthesis. *Plant, Cell & Environment* 24: 253–259.
- Bockheim JG, Everett LR, Hinkel KM, Nelson FE, Brown J. 1999. Soil organic carbon storage and distribution in Arctic Tundra, Barrow, Alaska. *Soil Science Society of America Journal* 63: 934–940.
- van Bodegom PM, Douma JC, Verheijen LM. 2014. A fully traits-based approach to modeling global vegetation distribution. *Proceedings of the National Academy of Sciences, USA* 111: 13733–13738.
- Boesgaard KS, Albert KR, Ro-Poulsen H, Michelsen A, Mikkelsen TN, Schmidt NM. 2012. Long-term structural canopy changes sustain net photosynthesis per ground area in high arctic *Vaccinium uliginosum* exposed to changes in near-ambient UV-B levels. *Physiologia Plantarum* 145: 540–550.
- Bonan GB, Lawrence PJ, Oleson KW, Levis S, Jung M, Reichstein M, Lawrence DM, Swenson SC. 2011. Improving canopy processes in the Community Land Model version 4 (CLM4) using global flux fields empirically inferred from FLUXNET data. *Journal of Geophysical Research–Biogeosciences* 116: G02014.
- Brown J, Everett KR, Webber PJ, Maclean SF, Murray DF. 1980. The coastal tundra at Barrow. In: Brown J, Miller PC, Tiezen LL, Bunnell FL, eds. *An Arctic ecosystem: the coastal tundra at Barrow, Alaska*. Stroudsburg, PA, USA: Dowden, Hutchinson & Ross, 1–29.
- von Caemmerer S. 2000. *Biochemical models of leaf photosynthesis*. Collingwood, Australia: CSIRO Publishing.
- Chapin FS, Bretharte MS, Hobbie SE, Zhong HL. 1996. Plant functional types as predictors of transient responses of arctic vegetation to global change. *Journal of Vegetation Science* 7: 347–358.
- Chapin FS, Shaver GR. 1996. Physiological and growth responses of arctic plants to a field experiment simulating climatic change. *Ecology* 77: 822–840.
- Chapin FS, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre JA. 1995. Response of Arctic tundra to experimental and observed changes in climate. *Ecology* 76: 694–711.
- Chapin FS, Van Cleve K, Tieszen LL. 1975. Seasonal nutrient dynamics of tundra vegetation at Barrow, Alaska. *Arctic and Alpine Research* 7: 209–226.
- Collatz GJ, Ball JT, Grivet C, Berry JA. 1991. Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration – a model that includes a laminar boundary layer. *Agricultural and Forest Meteorology* 54: 107–136.
- Croft H, Chen JM, Luo X, Bartlett P, Chen B, Staebler RM. 2017. Leaf chlorophyll content as a proxy for leaf photosynthetic capacity. *Global Change Biology* 23: 3433–3964.
- De Kauwe MG, Lin YS, Wright IJ, Medlyn BE, Crous KY, Ellsworth DS, Maire V, Prentice IC, Atkin OK, Rogers A *et al.* 2016. A test of the 'one-point method' for estimating maximum carboxylation capacity from field-measured, light-saturated photosynthesis. *New Phytologist* 210: 1130–1144.
- Dietze MC, Serbin SP, Davidson C, Desai AR, Feng X, Kelly R, Kooper R, LeBauer D, Mantoath J, McHenry K *et al.* 2014. A quantitative assessment of



- a terrestrial biosphere model's data needs across North American biomes. *Journal of Geophysical Research-Biogeosciences* 119: 286–300.
- Dubois JJ, Fiscus BEL, Booker FL, Flowers MD, Reid CD. 2007. Optimizing the statistical estimation of the parameters of the Farquhar–von Caemmerer–Berry model of photosynthesis. *New Phytologist* 176: 402–414.
- Ethier GJ, Livingston NJ. 2004. On the need to incorporate sensitivity to CO<sub>2</sub> transfer conductance into the Farquhar–von Caemmerer–Berry leaf photosynthesis model. *Plant, Cell & Environment* 27: 137–153.
- Farquhar GD, Caemmerer SV, Berry JA. 1980. A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species. *Planta* 149: 78–90.
- Feng XH, Dietze M. 2013. Scale dependence in the effects of leaf ecophysiological traits on photosynthesis: Bayesian parameterization of photosynthesis models. *New Phytologist* 200: 1132–1144.
- Fisher JB, Badgley G, Blyth E. 2012. Global nutrient limitation in terrestrial vegetation. *Global Biogeochemical Cycles* 26: GB3007.
- Fisher JB, Sikka M, Oechel WC, Huntzinger DN, Melton JR, Koven CD, Ahlstrom A, Arain MA, Baker I, Chen JM *et al.* 2014. Carbon cycle uncertainty in the Alaskan Arctic. *Biogeosciences* 11: 4271–4288.
- Fletcher BJ, Gornall JL, Poyatos R, Press MC, Stoy PC, Huntley B, Baxter R, Phoenix GK. 2012. Photosynthesis and productivity in heterogeneous arctic tundra: consequences for ecosystem function of mixing vegetation types at stand edges. *Journal of Ecology* 100: 441–451.
- Flexas J, Diaz-Espejo A, Berry JA, Cifre J, Galmes J, Kaidenhoff R, Medrano H, Ribas-Carbo M. 2007. Analysis of leakage in IRGA's leaf chambers of open gas exchange systems: quantification and its effects in photosynthesis parameterization. *Journal of Experimental Botany* 58: 1533–1543.
- Friedlingstein P, Cox P, Betts R, Bopp L, Von Bloh W, Brovkin V, Cadule P, Doney S, Eby M, Fung I *et al.* 2006. Climate-carbon cycle feedback analysis: results from the C<sup>4</sup>MIP model intercomparison. *Journal of Climate* 19: 3337–3353.
- Friedlingstein P, Meinshausen M, Arora VK, Jones CD, Anav A, Liddicoat SK, Knutti R. 2014. Uncertainties in CMIP5 climate projections due to carbon cycle feedbacks. *Journal of Climate* 27: 511–526.
- Friend AD. 1995. PGEN – an integrated model of leaf photosynthesis, transpiration and conductance. *Ecological Modelling* 77: 233–255.
- Friend AD. 2010. Terrestrial plant production and climate change. *Journal of Experimental Botany* 61: 1293–1309.
- Friend AD, Kiang NY. 2005. Land surface model development for the GISS GCM: effects of improved canopy physiology on simulated climate. *Journal of Climate* 18: 2883–2902.
- Frost GV, Epstein HE. 2014. Tall shrub and tree expansion in Siberian tundra ecotones since the 1960s. *Global Change Biology* 20: 1264–1277.
- Galmes J, Hermida-Carrera C, Laanisto L, Niinemets U. 2016. A compendium of temperature responses of Rubisco kinetic traits: variability among and within photosynthetic groups and impacts on photosynthesis modeling. *Journal of Experimental Botany* 67: 5067–5091.
- Gu LH, Pallardy SG, Tu K, Law BE, Wullschlegel SD. 2010. Reliable estimation of biochemical parameters from C<sub>3</sub> leaf photosynthesis-intercellular carbon dioxide response curves. *Plant, Cell & Environment* 33: 1852–1874.
- Heskel MA, Bitterman D, Atkin OK, Turnbull MH, Griffin KL. 2014. Seasonality of foliar respiration in two dominant plant species from the Arctic tundra: response to long-term warming and short-term temperature variability. *Functional Plant Biology* 41: 287–300.
- IPCC. 2013. Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM, eds. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK and New York, NY, USA: Cambridge University Press.
- Iversen CM, Sloan VL, Sullivan PF, Euskirchen ES, McGuire AD, Norby RJ, Walker AP, Warren JM, Wullschlegel SD. 2015. The unseen iceberg: plant roots in arctic tundra. *New Phytologist* 205: 34–58.
- James RA, Munns R, Von Caemmerer S, Trejo C, Miller C, Condon T. 2006. Photosynthetic capacity is related to the cellular and subcellular partitioning of Na<sup>+</sup>, K<sup>+</sup> and Cl<sup>−</sup> in salt-affected barley and durum wheat. *Plant, Cell & Environment* 29: 2185–2197.
- Jorgenson MT, Shur YL, Pullman ER. 2006. Abrupt increase in permafrost degradation in Arctic Alaska. *Geophysical Research Letters* 33: L02503.
- Kattge J, Diaz S, Lavorel S, Prentice C, Leadley P, Boenisch G, Garnier E, Westoby M, Reich PB, Wright IJ *et al.* 2011. TRY – a global database of plant traits. *Global Change Biology* 17: 2905–2935.
- Kattge J, Knorr W. 2007. Temperature acclimation in a biochemical model of photosynthesis: a reanalysis of data from 36 species. *Plant, Cell & Environment* 30: 1176–1190.
- Kattge J, Knorr W, Raddatz T, Wirth C. 2009. Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. *Global Change Biology* 15: 976–991.
- Kaufman DS, Schneider DP, McKay NP, Ammann CM, Bradley RS, Briffa KR, Miller GH, Otto-Bliesner BL, Overpeck JT, Vinther BM *et al.* 2009. Recent warming reverses long-term Arctic cooling. *Science* 325: 1236–1239.
- Koven CD, Schuur EAG, Schaedel C, Bohn TJ, Burke EJ, Chen G, Chen X, Ciais P, Grosse G, Harden JW *et al.* 2015. A simplified, data-constrained approach to estimate the permafrost carbon-climate feedback. *Philosophical Transactions of the Royal Society A: Mathematical Physical and Engineering Sciences* 373: 20140423.
- Kull O, Kruijt B. 1998. Leaf photosynthetic light response: a mechanistic model for scaling photosynthesis to leaves and canopies. *Functional Ecology* 12: 767–777.
- Lebauer DS, Wang D, Richter KT, Davidson CC, Dietze MC. 2013. Facilitating feedbacks between field measurements and ecosystem models. *Ecological Monographs* 83: 133–154.
- Leffler AJ, Welker JM. 2013. Long-term increases in snow pack elevate leaf N and photosynthesis in *Salix arctica*: responses to a snow fence experiment in the High Arctic of NW Greenland. *Environmental Research Letters* 8: 025023.
- Long SP, Bernacchi CJ. 2003. Gas exchange measurements, what can they tell us about the underlying limitations to photosynthesis? Procedures and sources of error. *Journal of Experimental Botany* 54: 2393–2401.
- Lu J, Ji J. 2006. A simulation and mechanism analysis of long-term variations at land surface over arid/semi-arid area in north China. *Journal of Geophysical Research-Atmospheres* 111: D09306.
- Medlyn BE, Badeck FW, De Pury DGG, Barton CVM, Broadmeadow M, Ceulemans R, De Angelis P, Forstreuter M, Jach ME, Kellomaki S *et al.* 1999. Effects of elevated CO<sub>2</sub> on photosynthesis in European forest species: a meta-analysis of model parameters. *Plant, Cell & Environment* 22: 1475–1495.
- Medlyn BE, Dreyer E, Ellsworth D, Forstreuter M, Harley PC, Kirschbaum MUF, Le Roux X, Montpied P, Strassmeyer J, Walcroft A *et al.* 2002. Temperature response of parameters of a biochemically based model of photosynthesis. II. A review of experimental data. *Plant, Cell & Environment* 25: 1167–1179.
- Muraoka H, Noda H, Uchida M, Ohtsuka T, Koizumi H, Nakatsubo T. 2008. Photosynthetic characteristics and biomass distribution of the dominant vascular plant species in a high Arctic tundra ecosystem, Ny-Ålesund Svalbard: implications for their role in ecosystem carbon gain. *Journal of Plant Research* 121: 137–145.
- Muraoka H, Uchida M, Mishio M, Nakatsubo T, Kanda H, Koizumi H. 2002. Leaf photosynthetic characteristics and net primary production of the polar willow (*Salix polaris*) in a high arctic polar semi-desert, Ny-Ålesund, Svalbard. *Canadian Journal of Botany-Revue Canadienne de Botanique* 80: 1193–1202.
- Oleson KW, Lawrence DM, Bonan GB, Drewniak B, Huang M, Koven CD, Levis S, Li F, Riley WJ, Subin ZM *et al.* 2013. *Technical description of version 4.5 of the community land model (CLM)*. Boulder, CO, USA: National Center for Atmospheric Research.
- Patankar R, Mortazavi B, Oberbauer SF, Starr G. 2013. Diurnal patterns of gas-exchange and metabolic pools in tundra plants during three phases of the arctic growing season. *Ecology and Evolution* 3: 375–388.
- Price KV, Storn RM, Lampinen JA. 2006. *Differential evolution: a practical approach to global optimization*. New York, NY, USA: Springer.
- R Development Core Team. 2013. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. [WWW document] URL [www.r-project.org](http://www.r-project.org) [accessed October 2016].
- Reich PB, Oleksyn J, Wright IJ. 2009. Leaf phosphorus influences the photosynthesis–nitrogen relation: a cross-biome analysis of 314 species. *Oecologia* 160: 207–212.
- Rogers A. 2014. The use and misuse of V<sub>c,max</sub> in Earth System Models. *Photosynthesis Research* 119: 15–29.

- Rogers A, Ely KS, Serbin SP. 2017a. Leaf photosynthetic parameters  $V_{\text{cmax}}$  and  $J_{\text{max}}$  and supporting gas exchange data, Barrow, Alaska, 2012–2016. In: *Next generation ecosystems experiment Arctic data collection*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, TN, USA. [WWW document] URL doi: 10.5440/1336809 [accessed 1 January 2017].
- Rogers A, Ely KS, Serbin SP, Lasota S, Liberman-Cribbin W. 2017b. Leaf mass area, leaf carbon and nitrogen content, Barrow, Alaska, beginning 2012. In: *Next generation ecosystems experiments Arctic data collection*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, TN, USA. [WWW document] URL doi: 10.5440/1336812 [accessed 1 January 2017]. [Correction added after online publication 6 September 2017: the doi in Rogers *et al.* (2017b) has been corrected.]
- Rogers A, Medlyn BE, Dukes JS, Bonan G, von Caemmerer S, Dietze MC, Kattge J, Leakey ADB, Mercado LM, Niinemets Ü *et al.* 2017c. A roadmap for improving the representation of photosynthesis in Earth system models. *New Phytologist* 213: 22–42.
- Saarninen T, Rasmus S, Lundell R, Kauppinen OK, Hanninen H. 2016. Photosynthetic and phenological responses of dwarf shrubs to the depth and properties of snow. *Oikos* 125: 364–373.
- Salmon VG, Soucy P, Mauritz M, Celis G, Natali SM, Mack MC, Schuur EAG. 2016. Nitrogen availability increases in a tundra ecosystem during five years of experimental permafrost thaw. *Global Change Biology* 22: 1927–1941.
- Sargsyan K, Safta C, Najm HN, Debusschere BJ, Ricciuto D, Thornton P. 2014. Dimensionality reduction for complex models via bayesian compressive sensing. *International Journal for Uncertainty Quantification* 4: 63–93.
- Schuur EAG, McGuire AD, Schaedel C, Grosse G, Harden JW, Hayes DJ, Hugelius G, Koven CD, Kuhry P, Lawrence DM *et al.* 2015. Climate change and the permafrost carbon feedback. *Nature* 520: 171–179.
- Schuur EAG, Vogel JG, Crummer KG, Lee H, Sickman JO, Osterkamp TE. 2009. The effect of permafrost thaw on old carbon release and net carbon exchange from tundra. *Nature* 459: 556–559.
- Serbin SP, Dillaway DN, Kruger EL, Townsend PA. 2012. Leaf optical properties reflect variation in photosynthetic metabolism and its sensitivity to temperature. *Journal of Experimental Botany* 63: 489–502.
- Sharkey TD. 1985. Photosynthesis in intact leaves of  $C_3$  plants – physics, physiology and rate limitations. *Botanical Review* 51: 53–105.
- Sharkey TD, Bernacchi CJ, Farquhar GD, Singsaas EL. 2007. Fitting photosynthetic carbon dioxide response curves for  $C_3$  leaves. *Plant, Cell & Environment* 30: 1035–1040.
- Shaver GR, Chapin FS. 1980. Response to fertilization by various plant-growth forms in an Alaskan tundra – nutrient accumulation and growth. *Ecology* 61: 662–675.
- Shaver GR, Chapin FS, Billings WD. 1979. Ecotypic differentiation in *Carex aquatilis* on ice-wedge polygons in the Alaskan coastal tundra. *Journal of Ecology* 67: 1025–1046.
- Shiklomanov NI, Streletskiy DA, Nelson FE, Hollister RD, Romanovsky VE, Tweedie CE, Bockheim JG, Brown J. 2010. Decadal variations of active-layer thickness in moisture-controlled landscapes, Barrow, Alaska. *Journal of Geophysical Research-Biogeosciences* 115: G00104.
- Smith NG, Dukes JS. 2013. Plant respiration and photosynthesis in global-scale models: incorporating acclimation to temperature and  $\text{CO}_2$ . *Global Change Biology* 19: 45–63.
- Souther S, Fetcher N, Fowler Z, Shaver GR, McGraw JB. 2014. Ecotypic differentiation in photosynthesis and growth of *Eriophorum vaginatum* along a latitudinal gradient in the Arctic tundra. *Botany-Botanique* 92: 551–561.
- Starr G, Neuman DS, Oberbauer SF. 2004. Ecophysiological analysis of two arctic sedges under reduced root temperatures. *Physiologia Plantarum* 120: 458–464.
- Starr G, Oberbauer SF. 2003. Photosynthesis of arctic evergreens under snow: implications for tundra ecosystem carbon balance. *Ecology* 84: 1415–1420.
- Sturm M, Racine C, Tape K. 2001. Climate change – increasing shrub abundance in the Arctic. *Nature* 411: 546–547.
- Tape K, Sturm M, Racine C. 2006. The evidence for shrub expansion in Northern Alaska and the Pan-Arctic. *Global Change Biology* 12: 686–702.
- Thornton PE, Zimmermann NE. 2007. An improved canopy integration scheme for a land surface model with prognostic canopy structure. *Journal of Climate* 20: 3902–3923.
- Torn M, Raz-Yaseef N, Billesbach D. 2014. Eddy-covariance and auxiliary measurements, NGEE-Barrow, 2012–2013. *Next generation ecosystem experiments – Arctic data collection*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, TN, USA. [WWW document] URL doi: 10.5440/1124200 [accessed 8 January 2014].
- Varhammar A, Wallin G, McLean CM, Dusenage ME, Medlyn BE, Hasper TB, Nsabimana D, Uddling J. 2015. Photosynthetic temperature responses of tree species in Rwanda: evidence of pronounced negative effects of high temperature in montane rainforest climax species. *New Phytologist* 206: 1000–1012.
- Walker AP, Beckerman AP, Gu LH, Kattge J, Cernusak LA, Domingues TF, Scales JC, Wohlfahrt G, Wullschlegel SD, Woodward FI. 2014. The relationship of leaf photosynthetic traits –  $V_{\text{cmax}}$  and  $J_{\text{max}}$  – to leaf nitrogen, leaf phosphorus, and specific leaf area: a meta-analysis and modeling study. *Ecology and Evolution* 4: 3218–3235.
- van de Weg MJ, Shaver GR, Salmon VG. 2013. Contrasting effects of long term versus short-term nitrogen addition on photosynthesis and respiration in the Arctic. *Plant Ecology* 214: 1273–1286.
- Wookey PA, Robinson CH, Parsons AN, Welker JM, Press MC, Callaghan TV, Lee JA. 1995. Environmental constraints on the growth, photosynthesis and reproductive development of *Dryas octopetala* at a high Arctic polar semidesert, Svalbard. *Oecologia* 102: 478–489.
- Wullschlegel SD. 1993. Biochemical limitations to carbon assimilation in  $C_3$  plants – a retrospective analysis of the  $A/C_i$  curves from 109 species. *Journal of Experimental Botany* 44: 907–920.
- Wullschlegel SD, Epstein HE, Box EO, Euskirchen ES, Goswami S, Iversen CM, Kattge J, Norby RJ, van Bodegom PM, Xu X. 2014. Plant functional types in Earth system models: past experiences and future directions for application of dynamic vegetation models in high-latitude ecosystems. *Annals of Botany* 114: 1–16.
- Xu CG, Fisher R, Wullschlegel SD, Wilson CJ, Cai M, McDowell NG. 2012. Toward a mechanistic modeling of nitrogen limitation on vegetation dynamics. *PLoS ONE* 7: e37914.
- Zhu C, Ziska L, Zhu J, Zeng Q, Xie Z, Tang H, Jia X, Hasegawa T. 2012. The temporal and species dynamics of photosynthetic acclimation in flag leaves of rice (*Oryza sativa*) and wheat (*Triticum aestivum*) under elevated carbon dioxide. *Physiologia Plantarum* 145: 395–405.
- Ziehn T, Kattge J, Knorr W, Scholze M. 2011. Improving the predictability of global  $\text{CO}_2$  assimilation rates under climate change. *Geophysical Research Letters* 38: 10404.